THE
AMERICAN NATURALIST

Vol. LII. *August–September, 1918* Nos. 620–621

THE RELATION BETWEEN COLOR AND OTHER CHARACTERS IN CERTAIN AVENA CROSSES[1]

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Species crosses among oats have not been studied to any great extent, yet they offer some very interesting problems. Trabut[2] says:

> Hybridization between the cultivated species of oats has not yet been methodically attempted to my knowledge, and there is here a very interesting open field. It is true that we have yet to determine in what degree a true hybridization will be possible. If *Avena fatua sativa* may be crossed with *A. sterilis culta*, a progeny may be produced having very useful mixed characters. *A. abyssinica* will gain by being crossed with the really superior *A. strigosa*. But in the matter of hybridization there is much more to be gained from experimentation than from the mere discussion of theoretical views.

Since this paper was read (1911) some studies have been reported on with different species crosses in oats. Zade[3] discusses results obtained from a cross between *fatua* and *sativa*. He found F_1 to be intermediate and that the F_2 gave types resembling *fatua, sativa,* and the F_1 intermediate type. These with respect to awns and hairs gave a 1:2:1 ratio.

Surface[4] has described rather fully some results ob-

[1] Paper No. 70, Department of Plant Breeding, Cornell University, Ithaca, N. Y.

[2] *Journal of Heredity,* Vol. 5, pp. 84–85, 1914. (Translated from the original article published 1912.)

[3] Der Flughofer, *Deut. Landw. Gesell. Ab.*, 279: 1–91, 1912.

[4] *Genetics,* Vol. 1, No. 3, pp. 252–286, May, 1916.

tained from a cross between *Avena fatua* × *Avena sativa* var. Kherson. The two parent forms differ in a number of characters some of which may be given here. The *Avena fatua* is brown or black in color, has both kernels awned and pubescent and has the typical wild type of base surrounded by a tuft of basal hairs. The Kherson is yellow in color, has few or no awns and lacks pubescence on the glumes and has the typical *sativa* base on which is found an occasional hair.

The F_1 type is intermediate between the two parents. The color of grain is brown but somewhat lighter than the wild parent, and the larger kernel in the spikelet is usually awned,[5] while the smaller or upper kernel is never awned. The lower grain exhibits a medium pubescence while the upper grain is always smooth. The base is intermediate between the two parent forms with tufts of hair on each side but not all around the base.

Some of the results of the F_2 generation may be given in Surface's conclusion:

> The data show that the wild parents carry genes for gray and probably for yellow color in addition to the black. These three colors segregate independently of each other. The observed ratio closely approximates the expected and confirms Nilsson-Ehle's conclusions.
>
> The cultivated base of the grain is dominant to the wild and segregates independently of the color genes. The heterozygous condition in the lower grain can be recognized in the majority of plants.
>
> In this cross seven pairs of characters are completely correlated with the character of the base. The characters associated with the wild base are (1) heavy awn on the lower grain, (2) awns on the upper grain, (3) wild base on the upper grain, (4) pubescence on the pedicel on the lower, and (5) on the upper grain, (6) pubescence on all sides of the base of the lower grain and (7) pubescence on the base of the upper grain.
>
> The gene for pubescence on the back of the lower grain is partially linked with the black color factor. The F_2 generation is too small to determine the exact degree of linkage but indicates that there are about 0.7 per cent. of crossovers.

[5] Surface, on page 258 of *Genetics,* Vol. 1, No. 3, 1916, says, "the majority of the lower grains show a weak, straight awn" and on page 265 says "the majority of F_1 spikelets show no awn whatever." It is not clear just which is meant.

The gene for pubescence on the back of the upper grain segregates independently of the color factor except that in the absence of the gene for pubescence on the lower grain the gene for pubescence on the upper is unable to act. In this sense the gene for pubescnce on the lower grain is a basic pubescence factor similar to the color factor (C) found in many animals and plants.

Material and Methods

The present authors have been working with oat species crosses for several years. A number of different combinations have been made and studied, including several species and many of their derivatives. It is planned here to emphasize certain results obtained with a cross between *Avena fatua* and *Avena sativa* var. Sixty Day. This Sixty Day variety is identical with the Kherson as used by Surface so far as general varietal characteristics are concerned, yet no doubt there are many strains of both sorts.

The *Avena fatua* in appearance was similar to the type used by Surface and has the characters described above. The Sixty Day oat is yellow and seldom do any awns appear. There are no dorsal hairs but an occasional basal hair may be found.

The plants used in making these crosses were grown in the greenhouse since a greater number of successful pollinations can be made than when the plants are grown in the field. The *Avena fatua* was used as the female parent and a number of flowers were emasculated and pollinated. Three seeds developed and each produced a plant. The F_1 generation plants were also grown in the greenhouse since they may receive greater care and more seed may be obtained. All later generations were grown in the field, spacing the plants two to three inches in the rows.

Discussion of Results

The F_1 type was as described by Surface, generally intermediate in type. The color was brown somewhat lighter than the wild type. The large kernel of the spikelet was often awned and was covered with dorsal

hairs. The small kernel of the spikelet was never awned but had an occasional sprinkling of dorsal hairs. The base was more like the *sativa* type, yet appeared to be more intermediate in type with some basal hairs on either side of the base but not at the back.

When the seeds from the first generation plants were sown, a number of different types appeared in the second generation. There were some that resembled the two parent forms and also other types different in color, amount of awning, pubescence, and the like.

As regards color there appeared four types, black, gray, yellow and white. The white ones, of which there were only four, were tested later and proved to be gray, thus leaving only the three color types. The black oats were of two general types, those having the two strong awns and pubescence on both kernels and the wild base, and those having pubescence on the large kernel and sometimes on the small one and with an intermediate or *sativa* type of base. Some of these forms were awnless and others possessed varying amounts of awn which were in some cases strong and in others weak.

The gray colored oats were both pubescent and smooth, some fully awned, some partially awned, and some awnless. They also segregated as to type of base.

The yellow oats, however, were all smooth and possessed very few or no awns. No yellow oats developed the strong awns similar to the wild type.

The segregation as to color and percentage of awns of the second generation plants is shown in Table I.

TABLE I

SHOWING THE SEGREGATION AS TO COLOR AND PERCENTAGE OF AWNS. SERIES 687, *Avena fatua* × *Avena sativa* VAR. SIXTY DAY

Percentage of Awns

Color	0	1–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100	Totals
Black....	46	25	20	23	12	17	21	23	14	8	2	99	310
Gray.....	11	9	6	10	3	10	6	5	1	3		28	92
Yellow...	9	7	1	1									18
Totals..	66	41	27	34	15	27	27	28	15	11	2	127	420

The percentage of awns was determined by taking a typical head from each plant and counting the total number of spikelets and the number of awned spikelets, and then determining the percentage of awned spikelets. Since there are a number of plants having no awns and also a number having 100 per cent. it seems best to arrange the classes as has been done in this table; that is, separate classes have been made for the 0 and 100 per cent. values.

From this table it is clear that the black oats possessed varying degrees of the awned condition from awnless to fully awned. The grays too showed about the same range of distribution. The yellow types, however, showed a tendency to be grouped in the lower classes. No yellow types were found having more than 30 per cent. of awns. It seems quite evident that there may be some relation between the yellow oat and the lack of awning.

Nilsson-Ehle[6] has discussed a case of a cross in oats where there was an apparent inhibition of awning produced by a yellow oat. He concludes that there was some inhibitory effect of the yellow color or that the yellow color factor acted also as an inhibitor of awns. The oats Nilsson-Ehle worked with were domestic types and it is a well-known fact that the domestic sorts vary as to the amount of awns with the change in environment. For that reason it is felt that results obtained from wild crosses will be more definite since the wild type produces its fully awned condition under very diverse growth conditions. This is all the more evident from a cross of this same Sixty Day type used in these crosses with a black cultivated oat. It was found that the yellow oats segregating from this cross contained fewer awns than did the blacks, whites, and grays but that the percentage of awns on the black parent was so variable that the results obtained are not definite. Such is not the case for the awning of the *Avena fatua* as stated above.

[6] *Zeitschrift für induktive Abstammungs- und Vererbungslehre*, Bd. XII, Heft 1, 1914.

These results show that the segregation as to color, as mentioned above, produces three types, black, gray and yellow. On the assumption that the wild oat carries genes for black, gray and yellow we would expect a segregation of 12 black : 3 gray : 1 yellow. These figures approach this result, but there are too few yellows and too many grays. Instead of the numbers obtained we expect 315.00 blacks : 78.75 grays : 26.25 yellows. It is very difficult to always distinguish between pale grays, yellows and whites, a fact which is well known to those working with oats. This is especially true in unfavorable seasons when oats are likely to weather badly. No doubt this difficulty is one of the reasons for the deviation of the gray and yellow classes. When we group the non-blacks together we have a very fair approximation to the 3 : 1 ratio, which ratio would be expected on the above assumption.

The relation between color and pubescence for these same second generation plants is well illustrated by Table II.

TABLE II

SHOWING THE RELATION BETWEEN COLOR AND PUBESCENCE OF THE SECOND GENERATION PLANTS OF SERIES 687, *Avena fatua* × *Avena sativa* VAR. SIXTY DAY

Pubescence

Color	Both Kernels Pubescent	One Kernel Pubescent	Smooth	Totals
Black	112	198		310
Gray	26	42	24	92
Yellow			18	18
Totals	138	240	42	420

Certain interesting facts are brought out by this table. It is apparent that all of the black oats are pubescent, some having both kernels pubescent and a larger number having only the one kernel pubescent. It is very significant that there are no smooth black oats. The gray oats, on the other hand, have a certain number of which both kernels are pubescent, a larger number with one

kernel pubescent, and still another lot of smooth oats. It seems that the gray oats segregate as to pubescence on what may be a 1:2:1 ratio. Regarding the yellow oat it is very significant that all of them are in the smooth class. That is, no yellow oats are found which are pubescent. Certain ones which were found appeared yellow but which proved on testing to be gray instead of yellow, so that at present no true yellow oats which are pubescent have been obtained out of this cross.

From these data it seems without any doubt that yellow oats in some way or another tend to inhibit the factor for pubescent. It is also apparent that there is one factor for pubescence which is linked with the black color factor. There sems to be another factor for pubescence which is independent of any color factor and for this reason we obtain gray oats in approximately the ratio of 1:2:1 so far as pubescence is concerned. Owing to the inhibiting effect of the yellow oat, there are no pubescent forms obtained. From this material it is clear then that we are working with a *fatua* form which has two factors for pubescence, one of which is linked with the black color factor and one which is independent. More will be said regarding these facts later in this paper, when another cross will be mentioned.

Another interesting relationship is that shown between the color in the F_2 generation and the segregation as to type of base. As mentioned earlier in this paper, the type of base differs from the wild form which is the typical sucker-mouth shape while that of the cultivated oat is of the typical *sativa* form. The *sativa*-like form is dominant or partially so to the wild type. A study of this and a large number of other crosses in which the wild type has been used as one of the parents indicates that the segregation of the base follows the 1:3 ratio, wild being the recessive type.

The relation between color and type of base for the second generation plants of this cross is shown in Table III.

TABLE III

SHOWING THE SEGREGATION AS TO COLOR AND TYPE OF BASE. SERIES 687. *Aventa fatua* × *Avena sativa* VAR. SIXTY DAY

Type of Base

Color	Wild	Sativa	Totals
Black	97	213	310
Gray	26	66	92
Yellow		18	18
Totals	123	297	420

From this table it is clear that the black oats segregates into the wild and *sativa* forms as also do the grays. On the other hand, the yellow oats exhibit no wild type of base but are all of the *sativa* class. It is also apparent from these data, then, that in addition to the inhibition of awn production and pubescence there is also some factor or factors which inhibit the production of the wild type of base when this particular cross is made. That it must be due to some factor or factors related to the yellow oats is clear from the fact that with a large number of crosses in which white oats and other forms have been used, the grays and whites as well as the blacks exhibit the wild type of base in about the ratio that would be expected.

TABLE IV

SHOWING THE RELATION BETWEEN COLOR AND PERCENTAGE OF AWNS FOR THE THIRD GENERATION FAMILIES PRODUCED FROM THREE HETEROZYGOUS PLANTS OF THE SECOND GENERATION. SERIES 687. *Avena fatua* × *Avena sativa* VAR. SIXTY DAY

Percentage of Awns

Color	0	1–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100	Totals
Black	82	45	17	9	3	4	5	3	4			58	230
Gray	12	13	6	1	2	1	2	1		1		18	57
Yellow	10	7	2			1	1						21
Totals	104	65	25	10	5	6	8	4	4	1		76	308

Seed from a large number of F_2 plants were tested in the F_3 generation but all of these will not be discussed here. Three of these which exhibited the segregation

similar to that obtained in the F_2 generation have been brought together and the results are here shown for the three classifications made on the second generation.

The relation between color and percentage of awns of these three families mentioned above is shown in Table IV.

Here again, it is apparent that the black oats ranged all the way from awnless to 100 per cent. awns as do the gray oats. The yellow oats, on the other hand, are grouped near the lower percentage classes. Two individuals, however, exhibited about 50 per cent. of awns, one being in class 40 to 49, one in 50 to 59. It may be that these will be found to be grays instead of yellows. However, in general, the tendency is for the yellows to exhibit only a few awns. This is in accordance with the results obtained on the second generation and substantiates the conclusion drawn from the study of that material. It may be worth while to call attention here to the segregation as to color which fits the hypothesis more closely than does the material of the second generation. The segregation exhibits what is without doubt a 12 : 3 : 1 ratio. The observed numbers are 230 black : 57 gray : 21 yellows while the expected numbers are 231.00 blacks : 57.75 grays : 19.25 yellows.

The relation between color and pubescence on these third generation families is shown by Table V.

TABLE V

SHOWING THE SEGREGATION AS TO COLOR AND PUBESCENCE OF THREE F_3 FAMILIES GROWN FROM HETEROZYGOUS F_2 PLANTS. SERIES 687

Pubescence

Color	Both Kernels Pubescent	One Kernel Pubescent	Smooth	Totals
Black	91	139	—	230
Gray	19	12	26	57
Yellow	—	5	16	21
Totals	110	156	42	308

Here it is clear that again all the black oats are pubescent while the gray oats fall into the three classes. The

segregation of the grays does not follow the 1:2:1 ratio here but it is possible that some of those classed as non-pubescent may have a few hairs when examined more closely. It was found with the second generation material that it was necessary to use a lens with certain ones, especially where there was very little pubescence showing. This has not been done with all those in this table and, therefore, it is possible on later examination that some of them may fall into the group of one kernel pubescent. The yellow oats also, instead of all being in the non-pubescent group, have a few in the class having one kernel pubescent. It is likely that on later examination these will be found to be gray oats. This can not be said at present. In general, it may be said that this segregation agrees very closely with that of the second generation with the exception of the five yellow plants which seem to exhibit some slight amount of pubescence.

The relations between color and type of base for these same three third generation families is shown in Table VI.

TABLE VI

SHOWING THE RELATION BETWEEN COLOR AND TYPE OF BASE IN THREE THIRD GENERATION FAMILIES. SERIES 687, *Avena fatua* × *Avena sativa* VAR. SIXTY DAY

Type of Base

Color	Wild	Sativa	Totals
Black	57	173	230
Gray	18	39	57
Yellow		21	21
Totals	75	233	308

On examining this table it is clear that the segregation of these third generation families agrees very closely with that of the second generation material. The black and gray oats have both wild and *sativa* bases in apparently a 1:3 ratio. The yellow oats, on the other hand, have only the *sativa* base. This material tends to substantiate the conclusions drawn from the second generation material, which is to the effect that it does not seem

possible to produce a yellow oat from this cross having the type of base of the wild parent.

Further information may be had regarding pubescence and color on examining the results on three other third generation families which have been grouped according to color and pubescence. The parent plants which produced these three families were black, pubescent on one kernel and nearly awnless.

These results are shown in Table VII.

TABLE VII

SHOWING THE RELATION BETWEEN COLOR AND PUBESCENCE FROM THREE THIRD GENERATION FAMILIES OF SERIES 687, *Avena fatua* × *Avena sativa* VAR. SIXTY DAY

Pubescence

Color	One Kernel Pubescent	Smooth	Totals
Black	231		231
Yellow		88	88
Totals	231	88	319

The segregation shows that no gray was present and that the segregation is only for blacks and yellows so far as color is concerned and follows an approximate 3:1 ratio. In regard to the pubescence it is clear that all of the black oats are pubescent while all the non-blacks or yellows are smooth. This material further substantiates the statement made earlier in this discussion to the effect that there is a pubescent factor linked with the black oat.

GENERAL DISCUSSION

The foregoing data show that there is a very definite relation between color of glume and production of awns. On the black and gray oats awns are produced in varying amounts while few or no awns are produced on the yellow oats. Regarding the inheritance of awns, it has been shown[7] that the weak awn is inherited on a 1:3 ratio, the fully awned condition being recessive. The data

[7] Love, H. H., and Fraser, A. C., "The Inheritance of the Weak Awn in Certain Avena Crosses," AMER. NAT., 51, No. 608, August, 1917.

that have already been collected show also that the strong awn is inherited in the same manner. These data (Tables I and IV) give 203 fully awned : 525 partially awned or awnless, giving 2.92:1.12 per 4. We would expect on a 1:3 basis 182:546. The action of the yellow factor is to reduce the amount of awns on the yellow glumed oats.

It was stated earlier that there was apparently a pubescence factor linked with the black and also another pubescence factor which was not linked with any color. If this were true and there was no inhibitory effect produced by the yellow oats we would expect to obtain 15 pubescent to 1 non-pubescent form in the second generation. It may be well to state here that it has been found by experiment that the wild form used in this cross was of such a type that it had two factors for pubescence. We have also found another form which has only one factor for pubescence. When this form is crossed with a white oat, all of the non-blacks are smooth, showing that this form has the pubescence factor which is linked with the black while the forms having the two factors for pubescence give both pubescent and smooth non-blacks. This is well brought out by the data presented in Table VIII. Here the same white sort, Tartar King, was crossed with two forms of *Avena fatua*.

This table is made up of data of the second generation. It is possible that later experimentation may change the relationship of the colors particularly so far as the grays and whites are concerned. In these tables all those not showing blacks and grays are classed as yellows and whites. The further study of these has not proceeded far enough to determine just the relation here. It seems, without doubt, that we have two types of *fatua,* one giving the 15:1 ratio (Series 351a1) and one the 3:1 (Series 351b1). Again in the 3:1 distribution all the non-blacks are smooth.

It will be of interest here also to state when the type having one factor for pubescence was crossed with the Sixty Day type similar to the one used in Series 687 that all of the non-blacks, both grays and yellows, were

TABLE VIII

SHOWING THE SEGREGATION AS TO COLOR AND PUBESCENCE ON A CROSS BETWEEN *Avena fatua* and *Avena sativa*, VAR. TARTAR KING

Series 351a1 *Pubescence*

Color	Both Kernels Pubescent	One Kernel Pubescent	Smooth	Totals
Black	30	74		104
Gray	9	19	3	31
White and yellow	3	3	5	11
Totals	42	96	8	146
	$\underbrace{\qquad}_{138}$		8	

Series 351b1 *Pubescence*

Color	Both Kernels Pubescent	One Kernel Pubescent	Smooth	Totals
Black	72	144		216
Gray			61	61
White and yellow			18	18
Totals	72	144	79	295
	$\underbrace{\qquad}_{216}$		79	

smooth, showing that this form has the pubescence factor closely linked with the black color gene.

The results as obtained from Series 687 so far as color and pubescence are concerned may be explained in the following manner. We may assume the *Avena fatua* to be represented by BBGGYYPP, that is, possessing the factors black (B) which also produces pubescence, gray (G), yellow (Y) and another factor (P) for pubescence. The Sixty Day oat then may be bbggYYpp. We then assume Y to inhibit the production of pubescence in the absence of B or G.

It may also be well to state that the results here found can also be explained by assuming Y to have the effect of producing pubescence in the presence of G. We would then not assume any pubescence factor (P) for this explanation. This assumption would account for the results as well as the one chosen. On the other hand, from data already obtained on other crosses it does not

seem that this latter explanation is the one which should be used.

On the first hypothesis the F_1 individuals are, therefore, BbGgYYPp forming eight kinds of gametes. From this assumption then we would expect 48 black pubescent : 9 gray pubescent : 3 gray smooth : 4 yellow smooth. The ratio of pubescent to non-pubescent would be 57 : 7. The observed numbers in the second generation were 378 pubescent : 42 smooth. We would expect 374.06 pubescent : 45.94 smooth. The observed numbers from the three third generation families gave 266 pubescent : 42 smooth, while we would expect 274.31 : 33.69. Considering the two groups together we have 644 pubescent : 84 smooth, while we would expect 648,375 : 79.625. We see that the observed facts agree very well with the theory.

While it is not intended to go into details regarding the F_3 generation, it may be said that a number of observed facts tend to substantiate this hypothesis. For example, we should have some families segregating in the third generation giving 15 pubescent : 1 smooth. This we find to be so. Again we would, according to theory, expect to find some F_3 families segregating into blacks and grays where the grays would all be smooth. This we find also. We would also expect some gray oats to segregate into 9 pubescent : 7 smooth. This combination has also been found.

Regarding the base, it might be well to state that in studying the segregation of this series into the third and even into the fourth generation as yet no yellow oat has been found exhibiting the wild type of base. These results do not agree with those obtained by Surface although in general we might expect them to be similar since the yellow Sixty Day oat and the Kherson type are classed by some as the same variety of oat. Yet when we know that it is possible to obtain different strains out of a variety, particularly so far as the inheritance is concerned, it is not surprising that these results should not agree. Let us illustrate this by some results we have

obtained from crossing two black oats which by those studying classification of varieties of oats have been classed as the same variety and exhibit the same general botanical characters. When these two forms were crossed, both being black, the first generation plants were black but when the second generation was grown it was found that a segregation was obtained, giving 15 black to 1 non-black. This point then illustrates the statement made above that we shall probably obtain different segregations even though we are supposed to be using the same variety. This is also brought out by the fact that from the wild form, *Avena fatua,* we have been able to obtain different types so far as pubescence is concerned. How many other types may exist in the wild form of *fatua* we do not know, but experiments are underway to determine whether it is not possible to find other types as regards color and certain other characteristics.

From what is here said we do not intend to convey the idea that yellow color as found in oats will inhibit the production of awns, pubescence and base but mean merely that the yellow as exhibited in this series does that. In fact, we know from the crosses we have already studied where other yellow forms have been used that it is possible to obtain the yellow pubescent form and yellow ones with the wild base. Therefore, the statements made here hold only for the particular cross here reported.

Conclusion

The studies here presented show that we have some relation between these yellow oats and the absence of awns, pubescence, and the wild base. We also find that there are two types of pubescence, or better stated, two factors for pubescence, one of which is linked with black and one which is independent of any color factor. Owing to the inhibitory effect, we do not get a definite Mendelian ratio from these studies. It is also clear that the third generation material tends to substantiate the conclusion arrived at from the study of the second generation plants.